Introduced European smelt (*Osmerus eperlanus*) affects food web and fish community in a large Norwegian lake

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Abstract

Invasive and introduced fishes can affect recipient ecosystems and native species via altered competitive and predatory interactions, potentially leading to top-down and bottom-up cascading impacts. Here, we describe a case from a large lake in southern Norway, Storsjøen, where the illegal introduction of a small, predominantly planktivorous fish species, European smelt (*Osmerus eperlanus*), has led to changes in the native fish community and lake food web. Survey fishing data collected before (2007) and after (2016) the introduction indicates that smelt has become the numerically dominant fish species both in benthic and pelagic habitats, with concurrent reductions in the relative abundance of native European whitefish (*Coregonus lavaretus*) and Arctic charr (*Salvelinus alpinus*) populations. Stable isotope ($\delta^{13}C$ and $\delta^{15}N$) data indicate minor changes in the trophic niches of native whitefish and Arctic charr despite partly overlapping niches with the introduced smelt. In contrast, brown trout (*Salmo trutta*) showed an earlier shift to piscivory, a more pelagic niche and increased growth rate, likely because of the smelt induced increase in pelagic prey fish abundance. The main trophic pathway supporting top predators (i.e., large brown trout) in Storsjøen has, therefore, shifted from a littoral to a more pelagic base. Our study demonstrates that small-sized introduced fishes can alter lake food-web dynamics, with contrasting impacts on native fishes. This knowledge is vital for future evaluation and mitigation of potential impacts of smelt introductions on lake ecosystems.

Keywords: alien species, energy flow pathways, lake food web, predatory fish, resource competition, stable isotope analysis

Introduction

Invasive and introduced species are major global threats to biodiversity and ecosystem services (Rahel 2002; Pejchar and Mooney, 2009; Early et al. 2016). Besides potential negative impacts on the relative abundances of species in native communities, non-native species can trigger major changes in the structure and function of recipient ecosystems e.g. via altered food-web dynamics (e.g. Vander Zanden et al. 1999). In lakes, fish species that occupy intermediate trophic levels can have particularly important structuring roles due to their potential impacts on prey at lower trophic levels, competitors at the same trophic level and predators at the highest trophic levels (Amundsen et al. 2008; Wootton 2017). Hence, invasive planktivorous and/or benthivorous fish species are of major concern for lake management authorities, particularly if they develop high population densities and cause local extinctions of native species.

European smelt (*Osmerus eperlanus*; hereafter smelt) is a relatively small-sized, omnivorous fish species found in the lakes and coastal areas of western Europe. Smelt feed mainly on zooplankton, but also include zoobenthos and small conspecifics in their diet (Hammar et al. 2018). Smelt is typically the main food resource for large, pelagic predatory fishes, such as pikeperch (*Sander lucioperca*) and brown trout (*Salmo trutta*) and thus play a key role in the pelagic food-web compartment of many temperate lakes (e.g. Nyberg et al. 2001; Sandlund et al. 2005; Keskinen et al. 2012; Hammar et al. 2018). Compared to other examples of non-native pelagic fishes, such as vendace (*Coregonus albula*) in Europe (e.g. Bøhn et al. 2008; Bhat et al. 2014) and rainbow smelt (*Osmerus mordax*) in North America (e.g. Mercado-Silva et al. 2006; Gaeta et al. 2015), the potential impacts of introduced smelt on native fish communities and

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recipient lake ecosystems remains unexplored. Recent research from large Scandinavian lakes indicates that smelt can show variable life history strategies and large fluctuations in population size (Sandlund et al. 2017; Hammar et al. 2018). Such population fluctuations (cf. Strayer et al. 2017 for "boom-bust dynamics") have the potential to affect the niche use of generalist predatory fishes, although the expectation remains to be explored in ecosystems recently occupied by smelt.

Here, we studied the impacts of introduced smelt on the native fish community and lake food web of a large lake in southern Norway, Lake Storsjøen (hereafter Storsjøen). Based on genetic analyses, smelt was translocated to Storsjøen from a large, nearby lake Mjøsa, and first discovered by local fishermen in 2008 (Hagenlund et al. 2015). Since then, the smelt population has shown high reproductive success and population growth (Hagenlund et al. 2015), but their impacts on native fish species and the lake food web are not known. To study these potential impacts, we used comparable survey fishing and stable isotope data collected before (2007) and after (2016) the smelt introduction to Storsjøen. Stable isotope analysis (SIA) provides a powerful method to study temporally integrated variation in fish diets and the structure (e.g. food-chain length) and function (e.g. littoral *versus* pelagic energy flow pathways) of lake food webs (Post 2002; Boecklen et al. 2011; Layman et al. 2012). SIA has been widely used to study the impacts of invasive fishes on recipient ecosystems and native communities (e.g. Cucherousset et al. 2012 and references therein). Following the smelt introduction in Storsjøen, we expected that (1) the native planktivorous fish species, i.e. European whitefish (*Coregonus lavaretus*; hereafter whitefish) and Arctic charr (*Salvelinus alpinus*), would show decreased abundance but little change in their trophic niches, whereas the predominantly littoral benthivorous grayling (*Thymallus thymallus*) would remain unaffected. In contrast, we expected that (2) predatory brown trout would shift

to a more pelagic trophic niche, with an earlier onset of piscivory and increased growth rate due to the greater availability of small pelagic prey fish. Study results are further discussed in respect to potential long-term ecosystem impacts of the smelt introduction.

Materials and methods

Study lake

Lake Storsjøen is a large, deep, oligotrophic lake situated in Hedmark county, south-eastern Norway (Table 1). The lake is regulated for hydropower purposes at the lake outlet with a dam and it drains through the River Rena to Norway's largest river system, Glomma. Besides whitefish, Arctic charr, grayling and brown trout, the introduced smelt coexist with six other native fish species: pike (*Esox lucius*), perch (*Perca fluviatilis*), burbot (*Lota lota*), minnow (*Phoxinus phoxinus*), roach (*Rutilus rutilus*) and alpine bullhead (*Cottus poecilopus*).

Sample collection and preparation

The collection and preparation of fish samples were conducted according to permitting requirements of the Hedmark County Council and at the request of the hydropower company (Glommens og Laagens Brukseierforening) operating at Storsjøen. Fish were collected with survey gillnets in early summer and autumn in 2007 and 2016 (Online Resource 1). In each sampling period, the gillnets were set overnight (12–15-hr fishing time) in the littoral (0–10 m), profundal (>15 m) and pelagic (0–21 m below the surface) habitats. Both Jensen series consisting of single-mesh (knot-to-knot mesh sizes 6–52 mm) nets (Jensen 1977) and Nordic multi-mesh survey gillnets (12 panels of 2.5 m x 1.5 m with mesh sizes 5–55 mm; see Appelberg et al. 1995) were used in both seasons

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and years. In 2007, the benthic single-mesh gillnet series consisted of 12 nets (25 x 1.5 m) with mesh sizes of 6, 8, 10, 12.5, 16, 21, 26, 29, 35, 39, 45 and 52 mm, whereas only the nine largest mesh sizes (12.5–52 mm) were used in 2016. The floating pelagic gillnets were set at 0–6 and 15–21 m depth below the surface. The single-mesh floating gillnets were 25 x 6 m and they consisted of the same mesh sizes as the benthic gillnets (12 nets in 2007, nine nets in 2016). In 2016, pelagic sampling was extended with floating 27.5 x 6 m multi-mesh Nordic survey gillnets (11 mesh sizes of 6.25–55 mm) that were set at the same two depths as the single-mesh pelagic gillnets (see Online Resource 1 for more details of the survey fishing). The survey fishing data were used to evaluate between-year differences in habitat use and abundance of dominant fish species, based on catch per unit effort (CPUE) estimates calculated as number of fish caught per 100 m^2 of gillnet per night. To standardize the data between years, only catches in Nordic survey gillnets set in June 2007 and 2016 were included in CPUE calculations in the littoral and profundal habitats (see Fig.1 and Online Resource 1). Since no pelagic Nordic nets were set in 2007, the pelagic CPUE calculations were based on catches in the standard floating nets with 12–55 mm mesh set in June and August/September 2007 and 2016 (Fig.1 and Online Resource 1).

Each fish was identified, measured (standard length: ± 1 mm) and weighed (wet mass: ± 1.0 g). Scales were collected from each brown trout for subsequent growth analyses, conducted by back-calculation of the length at different ages prior to capture (Shearer 1992). From random subsamples of fish, the stomach and a small piece of dorsal muscle tissue were dissected, stored frozen at -20°C and later prepared for stomach contents (SCA) and stable isotope (SIA) analyses, respectively. Additional scale (n = 26 in 2007; n = 48 in 2016) and muscle tissue (n = 4 in 2007; n = 26 in 2016) samples of large brown trout (length = 260–800 mm) were collected from fish caught

148 during an annual trolling contest, “Storsjødreggen”, arranged in June 2007 and June
149 2016.

150 For SCA, the prey taxa were identified to genus, family or order level, and their
151 relative volumetric contributions to the stomach contents were estimated visually. The
152 prey taxa were later grouped as: (1) zooplankton (mainly *Daphnia* sp. and *Bosmina* sp.,
153 some *Holopedium* sp., *Cyclops* sp., *Heterocope* sp. and *Diaptomus* sp.), (2)
154 *Bythotrephes* sp. predatory cladocera, (3) zoobenthos (e.g. larvae of Chironomidae,
155 Trichoptera, Ephemeroptera and Plecoptera, Gastropoda, Dytiscidae), (4) surface
156 insects (adult stages of aquatic and terrestrial insects), (5) fish (mainly smelt but also
157 whitefish, minnow, alpine bullhead and perch), (6) fish eggs (mainly smelt eggs), and
158 (7) other unidentified prey. These prey groups were subsequently used to test for dietary
159 differences between the introduced smelt and the native whitefish, Arctic charr,
160 grayling and brown trout populations, as well as to compare the diets of whitefish,
161 grayling and brown trout between the two study years to evaluate potential smelt
162 impacts on resource use of native fishes.

163

164 ***Stable isotope analyses***

165 Littoral and pelagic basal resources and invertebrates were sampled on 1 August 2007
166 and 23 August 2016 for SIA to study the overall food-web structure in Storsjøen and to
167 provide baselines for isotopic mixing models reflecting the trophic niches of brown
168 trout, whitefish and grayling. Insufficient SIA data ($n \leq 2$ in one of the years) were
169 obtained from other native fishes, including Arctic charr, to conduct reliable between-
170 year comparisons of trophic niche changes following the smelt introduction. In 2007,
171 zooplankton and littoral benthic invertebrate samples were collected using a 60-µm
172 plankton net and a 500-µm mesh kick net, respectively. In 2016, benthic

macroinvertebrates were collected using a 500-µm mesh kick net and hand-picking in the shallow littoral areas (0–1 m depth) and a 243-µm mesh benthic sledge in the deep littoral (2–8 m) and profundal (20–34 m) areas. The macroinvertebrate samples were subsequently sieved through a 500-µm mesh. Pelagic zooplankton taxa were collected by taking several vertical hauls with an 80-µm plankton net throughout the uppermost 30 m of the water column. All benthic and pelagic invertebrates were sorted, cleaned of detritus and other unwanted material, identified to genus or family level and stored frozen at –20°C prior to final preparation for SIA. Only soft body tissue was dissected from mollusks and trichopterans with cases. Because only a few zooplankton (n = 2) and littoral benthic invertebrate (n = 5) samples were collected in 2007, the invertebrate SIA data from the two years were finally pooled to obtain more representative littoral and pelagic baselines and to account for spatial and temporal isotopic variation at low trophic levels (cf. Syväranta et al. 2006). Pooling of the invertebrate SIA data was supported by the absence of significant between-year differences in $\delta^{13}C$ values of *Lymnaea* sp. snails (W = 36, n = 18, P = 0.123), implying long-term stability of the littoral isotopic end-member.

All frozen fish and invertebrate SIA samples were later dried (for 48 h in an oven at 60°C in 2007 and in a freeze-drier in 2016) and homogenized using a mortar or a metallic pestle. The final SIA were performed at the Institute for Energy Technology (IFE; Kjeller, Norway) in 2007 and at the Environmental Isotope Laboratory (University of Waterloo, Canada) in 2016. Analytical precision was <0.3‰ for both $\delta^{13}C$ and $\delta^{15}N$, based on repeat analysis of an internal laboratory standard (2007) or duplicates (2016). See Sandlund et al. (2013) and Eloranta et al. (2016) for more details about the analytical procedures in Kjeller and Waterloo, respectively.

The relative trophic position (TP) of brown trout, whitefish and grayling in the food web of Storsjøen was estimated using the two-source isotopic mixing model described in Post (2002). The SIAR package (Stable Isotope Analysis in R; version 4.2; Parnell et al. 2010; Parnell and Jackson 2013) was used to estimate the reliance of whitefish, grayling, brown trout, Arctic charr and smelt populations on littoral *versus* pelagic carbon sources. To study ontogenetic dietary shifts of brown trout, the relative reliance of individuals on littoral carbon sources (LR) was estimated using the carbon isotope two-source mixing model described in Post (2002). The input data in TP, LR and SIAR computations included individual $\delta^{13}C$ and $\delta^{15}N$ values from fish muscle tissue and mean ± SD $\delta^{13}C$ and $\delta^{15}N$ values of littoral and pelagic invertebrates. In addition, the commonly used trophic fractionation corrections of 0.4 ± 1.3‰ for $\delta^{13}C$ and 3.4 ± 1.0‰ for $\delta^{15}N$ (Post 2002) were incorporated in SIAR computations.

We ran sensitivity analyses (see Online Resource 2) to see if our results from SIA data were influenced by the chosen trophic fractionation corrections or by lipid-normalization of the $\delta^{13}C$ values for fish with presumably high lipid content (i.e., C:N ratio >4). We found virtually no effect of different trophic fractionation corrections for the SIAR results. The main patterns in linear regression analyses of brown trout ontogenetic dietary shifts also remained the same after lipid-normalization, although the lipid-normalization did elevate and reduce individual variation in $\delta^{13}C$ values of large, piscivorous brown trout caught in 2016. As elaborated more in the Online Resource 2, we are confident that our main results based on SIA data are robust.

Statistical analyses

One-way non-parametric multivariate analyses of variance (NPMANOVA; see Anderson 2001) were performed in PAST program (Hammer et al. 2001) to test for

dietary differences between smelt, whitefish, Arctic charr, grayling and brown trout (samples pooled from both years). NPMANOVA was also used to test for between-year differences in diets of whitefish, grayling and brown trout, whereas no between-year comparisons were done for other fish species due to insufficient sample sizes. When significant ($P < 0.05$) dietary differences were observed in NPMANOVA, similarity percentage analysis (SIMPER) was used to determine which prey taxa contributed most to the dietary difference between species or years.

All other statistical analyses were performed in R v. 3.4.1 (R Core Team 2017) and key results are summarized in Table 2. Depending on the data normality and homoscedasticity, we used either parametric *t*-tests or non-parametric Mann-Whitney-Wilcoxon tests to test for between-year differences (2007 *versus* 2016) in standard length, Fulton's condition factor, $\delta^{13}C$ and TP of brown trout, whitefish and grayling caught with survey gillnets. For the same fish, we used Levene's test for the equality of variances to test for between-year differences in individual variation in $\delta^{13}C$ and TP. Taken together, analyses were expected to reflect the effects of smelt introduction on the size, nutrition, diet and trophic niche width (cf. Bearhop et al. 2004) of native fish species. Unfortunately, the available CPUE data did not allow any statistical comparisons because only the sampling location and period was reported and thus it was impossible to distinguish from which specific Nordic net each fish was removed. Moreover, due to limited resources available for the field work, only a few Nordic nets (n = 2–5) were set to each habitat in each period. Nevertheless, we believe that the available data of habitat use and relative abundance of different fish species provide important insights to the potential impacts of introduced smelt on the native fish community in Storsjøen.

In addition to between-species comparisons including all SIA data collected in both years, we compared the SIAR estimates of whitefish, grayling and brown trout sampled in 2007 and 2016 to test for potential trophic niche shifts following the smelt introduction. The *siarmcmcdirichletv4* function in the SIAR package (Parnell and Jackson 2013) was run with default settings (i.e., iterations = 200000, burnin = 50000, howmany = 10000, thinby = 15). The differences in the resulting SIAR estimates were considered statistically significant when the 95% Bayesian credibility intervals showed no overlap between the groups (i.e., species or years).

We used linear regression analysis to assess between-year differences in ontogenetic dietary shifts of brown trout. Specifically, we explored the effects of year (included as a factor) and individual length on brown trout trophic position (TP) and littoral reliance (LR). For both TP and LR, we fitted three linear regression models, all including log-transformed length as a covariate and year as either an additive effect, varying with length (interaction effect), or non-existing. The models were subsequently compared based on AICc values from the MuMIn package v.1.40.4 (Bartoń 2018). The most supported model (i.e., the lowest AICc score and ΔAICc > 2 compared to the second-best model) was chosen as the prediction model. We also checked for possible violations of the assumptions for the linear regression analysis. Two small individuals (<200 mm) with unexpectedly high TP were identified as outliers in the 2016 data and removed from the modelling dataset.

Finally, we used linear regression analysis to test for between-year differences in brown trout growth patterns. Here, brown trout length at the year of capture (y) was used as the response variable, while sampling year (included as a factor) as well as back-calculated length and age for the previous year (y–1) and their interaction were

used as explanatory variables. A few exceptionally old individuals (>10 years, n = 5) were excluded from the analyses to balance age structure between the years.

Results

The survey fishing data demonstrated changes in the Storsjøen fish community following the smelt introduction. Smelt became the numerically dominant fish species in the shallow littoral and deep profundal habitats, and equally abundant as whitefish in the pelagic habitat (Fig. 1a–c). The littoral catches of whitefish and Arctic charr seemed to decline, whereas brown trout apparently became more abundant and grayling remained unaffected in the littoral zone. The profundal catches showed somewhat contrasting patterns, since both whitefish and particularly burbot seemed to become more abundant in the catch following the smelt introduction. In contrast, the catches of previously relatively abundant Arctic charr apparently declined in both the profundal and pelagic habitats.

The SIA data (Fig. 2) indicate clear isotopic separation of the littoral and pelagic food-web compartments ($\delta^{13}C$) as well as consumers at different trophic levels ($\delta^{15}N$). The isotope biplots (Fig. 2) and the SIAR littoral reliance estimates (Fig. 3a) indicate that grayling and minnow are littoral benthivores whereas smelt and Arctic charr are heavily reliant on pelagic and/or profundal food resources. Whitefish and brown trout seem to have more generalist trophic niches and utilize both littoral and pelagic food resources. Piscivorous brown trout and burbot occupy the highest trophic position, but they also show the highest variation in $\delta^{13}C$ and $\delta^{15}N$, suggesting that some individuals are generalists while some others have specialized littoral or pelagic invertebrate or fish diets (Fig. 2).

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Whitefish and grayling showed no significant between-year differences (Table 2, Fig. 3b) in condition, trophic niche, and individual variation of $\delta^{13}C$ ($P > 0.150$). Grayling were larger (Table 2) and showed higher individual variation of TP in 2016 than in 2007 ($F_{1,28} = 15.33$, $P < 0.001$), but the latter might be partly due to larger sample size in 2016 (Table 2). The limited SIA data from Arctic charr indicated no shift in $\delta^{13}C$ and $\delta^{15}N$ values and a high niche overlap with the introduced smelt (Fig. 2 and 3).

The results from SIA were supported by SCA data indicating significant dietary segregation between smelt, whitefish, Arctic charr, grayling and brown trout (NPMANOVA: *pseudo* $F_{4,280} = 38.1$, $P < 0.001$; all pairwise comparisons: $P < 0.001$). Based on SIMPER results, the dietary segregation was mainly due to the zooplanktivorous diet of smelt, generalist diet of whitefish, dominance of *Bythotrephes* sp. in Arctic charr diet in 2007, and specialized benthivorous diet of grayling (Fig. 4), with the average between-species dissimilarities of main prey groups ranging from 26 to 48%. Brown trout and burbot were generalist piscivores that also fed on invertebrates, (Fig. 4). While prey fishes were not identified in 2007, the data from 2016 indicate that smelt of standard length 90–110 mm were the dominant prey fish for both brown trout and burbot. There were significant between-year differences in the diets of whitefish (*pseudo* $F_{1,89} = 3.7$, $P = 0.021$) and brown trout (*pseudo* $F_{1,75} = 3.5$, $P = 0.025$), but not of benthivorous grayling (*pseudo* $F_{1,22} = 1.0$, $P = 0.422$). According to SIMPER, the between-year differences resulted from decreased zooplanktivory and increased benthivory and egg-predation by whitefish, and from decreased consumption of surface insects and increased benthivory and piscivory by brown trout in 2016 following the smelt introduction (Fig. 4). While *Bythotrephes* sp. was the main dietary item for Arctic charr, and relatively common prey for whitefish and small brown trout in 2007, it was completely absent in fish stomachs analysed in 2016.

As hypothesized, brown trout shifted from littoral towards a more pelagic trophic niche following the smelt introduction, as indicated both by the SIAR estimates (Fig. 3b) and significantly lower $\delta^{13}C$ values in 2016 (Table 2). There were no corresponding between-year differences in brown trout size, condition and TP (Table 2), nor in individual variation of brown trout $\delta^{13}C$ and TP ($P > 0.100$). There were, however, clear between-year differences in ontogenetic (size-related) changes in brown trout trophic position (TP) and reliance on littoral carbon sources (LR). According to the most supported model for TP (Tables 3 and 4, Fig. 5a), brown trout underwent an ontogenetic shift to a higher trophic position (i.e., piscivory) at a smaller size in 2016 following the smelt introduction. The between-year difference in TP was particularly evident for brown trout larger than 300 mm. However, it should be noted that two small individuals (<150 mm) with exceptionally high TP were excluded from regression analysis, but they indicate that even very young and small brown trout had the potential to attain high TP in 2016 following the smelt introduction. For LR, two models were equally supported based on AIC ($\Delta AICc \sim 1.8$), but we selected the most supported and parsimonious (additive) model as the added interaction term in the second-best model seemed to be non-significant and give little extra information. Hence, the most supported model for LR included an additive effect of year (Tables 3 and 4, Fig. 5b), and predicted a generally lower reliance of brown trout on littoral food (i.e. carbon) resources in 2016 as compared to 2007, as well as a negative effect of length, indicating an ontogenetic shift from littoral towards a pelagic diet with increasing size. Finally, the linear regression model based on back-calculated length data indicated increased growth rate of brown trout following the smelt introduction, being particularly evident for large (>300 mm) and old (>5 years) individuals (Fig. 6, Table 5).

Discussion

The potential impacts of introduced European smelt on native fishes and recipient lake food webs have remained unexplored. Here, we have demonstrated that the predominantly planktivorous smelt can achieve high abundance and have contrasting impacts on native fishes soon after the introduction. Following the smelt introduction in Storsjøen, the relative abundance of predominantly pelagic Arctic charr and whitefish seems to have reduced, but their trophic niches have remained largely unaffected. No major changes in abundance or niche use were observed for littoral benthivorous grayling. In contrast, brown trout apparently became more abundant in the littoral zone and shifted earlier (i.e., at smaller size) to a pelagic, piscivorous trophic niche and grew better, likely due to the increased abundance of pelagic prey fish. Our study provides further evidence that introduced fishes occupying intermediate trophic levels can have high but contrasting impacts on native species and alter the energy mobilization pathways supporting top predators in lake ecosystems.

Our survey fishing data suggests that smelt has become the numerically dominant fish species in all major habitats in Storsjøen, as has the smelt source population in Lake Mjøsa (Sandlund et al. 1985a; Hagenlund et al. 2015). Whitefish and Arctic charr are among the most common fish species found in the pelagic and profundal habitats of large and deep lakes in northern Europe (e.g. Eloranta et al. 2015; Sandlund et al. 2010, 2016). These two salmonids are highly valued among commercial and recreational fishermen, but subjected to various anthropogenic disturbances such as warming, eutrophication, overfishing and invasion of competitive and predatory fishes, particularly in their southernmost distribution areas (e.g. Graham and Harrod 2009; Jeppesen et al. 2012). Although smelt in some cases might act as an important

368 pelagic prey species for Arctic charr (Hammar et al. 2018), the putative negative
369 impacts of smelt on coexisting fishes in Storsjøen likely result from strong competitive
370 and predatory interactions, as observed for invasive rainbow smelt in North American
371 lakes (e.g. Hrabik et al. 1998; Mercado-Silva et al. 2007). By being an efficient predator
372 of large-bodied cladocerans, smelt can reduce food availability and thereby reduce the
373 recruitment success of native pelagic fishes (e.g. Johnson and Goettl 1999; Beisner et
374 al. 2003; Mercado-Silva et al. 2007). In addition to resource competition, smelt may
375 have indirect negative impacts on whitefish and Arctic charr by facilitating faster
376 growth and earlier piscivory of brown trout, thereby increasing the number of predators
377 large enough to prey upon whitefish and Arctic charr. Large smelt can also have direct
378 predatory effects on small fish (Sandlund et al. 2005; Sletter et al. 2007) and affect lake
379 fish communities and food webs via intraguild predation and cannibalism, potentially
380 inducing smelt population fluctuations (cf. He and Labar 1994; Stetter et al. 2007;
381 Hammar et al. 2018). However, it should be noted that survey gillnet fishing (CPUE)
382 data are inherently sensitive to temporal and spatial fluctuations, inducing variation in
383 age distribution, year class strength and growth rate of different fish species. Hence,
384 future monitoring is needed to confirm whether the native whitefish and Arctic charr
385 populations in Storsjøen are truly declining due to the smelt introduction.

386 As compared to native pelagic fishes, smelt had minor or contrasting impacts
387 on native benthic fishes. Grayling are littoral benthivores (Eloranta et al. 2011) and
388 showed minor niche overlap with the more pelagic, planktivorous smelt. Besides niche
389 stability, the invariable grayling SIA values suggest minor between-year differences in
390 the littoral isotopic baseline. Due to missing SIA data from 2007, the potential impacts
391 of smelt introduction on the trophic niche of other benthic fishes remains unclear.
392 However, our limited CPUE and SCA data from burbot suggest increased utilization of

393 the deep profundal habitat and predation on smelt. Previous studies in nearby Lake
394 Mjøsa demonstrated that smelt can constitute 84–90% of fish prey in burbot stomachs
395 (Sandlund et al. 1985b). In our study, the observed intermediate and highly variable
396 isotopic values suggest that burbot are generalist predators that utilize both shallow-
397 and deep-water prey resources and hence integrate these spatially distinct lake habitats
398 and food-web compartments in Storsjøen (cf. Harrison et al. 2017). Increased burbot
399 abundance and predation may also contribute to the putative population decline of
400 Arctic charr, which commonly utilize the profundal zone as a refuge for intense
401 resource competition and predation (Eloranta et al. 2011, 2013; Sandlund et al. 2010,
402 2016).

403 Our findings provide further evidence that invasion of intermediate consumers
404 can alter lake food webs via altered competitive and predatory interactions (e.g. Vander
405 Zanden et al. 1999; Beisner et al. 2003; Rush et al. 2012). As indicated by the SIA data,
406 the main top predator in Storsjøen, brown trout, have shifted towards a more pelagic
407 trophic niche and become piscivorous at a smaller size than before smelt introduction.
408 As observed for predatory lake trout (*Salvelinus namaycush*) in North American lakes,
409 such alterations in littoral *versus* pelagic resource use can have marked consequences
410 ranging from individual (e.g. maximum and maturation size) to ecosystem (e.g.
411 coupling of habitats and food-web compartments) responses (McMeans et al. 2016).
412 Although we lack data for invertebrate communities and annual population fluctuations,
413 smelt may have affected community and food-web stability in Storsjøen via increased
414 competitive and predatory impacts as well as increased littoral–pelagic coupling by
415 predatory brown trout (cf. Schindler and Scheuerell 2002; Vander Zanden and
416 Vadeboncoeur 2002). Our data also demonstrates that the increased availability of
417 profitable pelagic prey fish (i.e., smelt) has led to an increase in annual growth of

predatory brown trout. These results concur with previous studies from North American lakes where the growth of native predatory walleye (*Sander vitreus*) increased substantially following invasion of pelagic rainbow smelt (Jones et al. 1994; Johnson and Goettl 1999). Although recreational fishermen seem content with the improved brown trout growth in Storsjøen, it remains to be seen whether the initial positive trends are followed by population declines of both smelt and brown trout, as observed in some North American lakes hosting rainbow smelt and predatory walleye (Johnson and Goettl 1999). The presumed seasonal and long-term fluctuations in abundance and niche use of smelt and predatory fishes (see e.g. Gaeta et al. 2015 and Hammar et al. 2018) calls for monitoring studies to examine the potential for cascading impacts on lower trophic levels, such as zooplankton abundance and community composition (e.g. Johnson and Goettl 1999).

To the best of our knowledge, this is the first stable isotope study demonstrating the impacts of introduced European smelt on native fishes and the recipient lake food web, although some recent studies have included limited examinations of linkages between introduced smelt and the native predatory and planktivorous fishes (Korlyakov and Mukhachev 2009; Sterligova and Ilmast 2017). The findings are highly relevant for the future evaluation, management and mitigation of environmental consequences associated with smelt introduction to Storsjøen as well as to other European lakes. However, our study lacks information about potential impacts on lower trophic levels, particularly on the abundance and composition of pelagic zooplankton but also littoral and profundal benthos. The available SCA data suggests that the large-sized *Bythotrephes* sp. cladoceran has disappeared or decreased in numbers, being one of the main prey for pelagic fishes in 2007, but completely absent from fish stomachs in 2016 following the smelt introduction. Disappearance of this zooplankton prey might have

443 contributed to the putative population declines of native planktivorous fishes,
444 particularly of Arctic charr whose stomach contents were dominated by *Bythotrephes*
445 sp. in 2007. Hence, annual monitoring of the invertebrate and fish communities would
446 provide a more holistic view of the potential whole ecosystem-level impacts and status
447 of native fish populations, particularly if combined with monitoring of water quality
448 and of a reference lake lacking smelt. Monitoring of the smelt population would also
449 enable detection of possible boom-and-bust cycles (cf. Strayer et al. 2017), as seen in
450 invasive rainbow smelt (Gorman 2007). Moreover, more comprehensive, including
451 seasonal, studies of diets and parasites of smelt and the coexisting native fishes would
452 provide valuable insights to the prevailing food-web dynamics in Storsjøen. Overall,
453 more research on the role of European smelt in lake ecosystems is urgently needed,
454 given the extent and complexity of impacts (e.g. top-down and bottom-up trophic
455 cascades, contaminant bioaccumulation) induced by its invasive sibling in North
456 American lakes, the rainbow smelt (e.g. Vander Zanden and Rasmussen 1996; Rooney
457 and Paterson 2009).

458 To conclude, our findings support previous studies demonstrating complex and
459 often unwanted impacts of introduced smelt on native fishes and lake ecosystems (see
460 e.g. Rooney and Paterson 2009 and references therein). Although smelt species are
461 profitable prey for predatory fish, they may induce major trophic cascades and reduce
462 recruitment success of some highly valued native fishes. To conserve the populations
463 of native pelagic salmonids (e.g. whitefish and Arctic charr) at their southern
464 distribution limits, it is essential to prevent new introductions and secondary spreading
465 of smelt. This is particularly true in temperate lakes which are also subjected to other
466 anthropogenic disturbances such as eutrophication, acidification and water level
467 regulation for hydropower (Dudgeon et al. 2006; Hirsch et al. 2017). Overall, improved

468 management and monitoring of lakes invaded by European smelt is a necessity for
469 successful mitigation of the potential negative impacts. Yet, total removal of the
470 European smelt would likely prove impossible as realized with its invasive sibling in
471 North American lakes (Gaeta et al. 2015).
472

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Tables

Table 1 Characteristics of the study lake, Storsjøen, southeastern Norway. *Analysed from a surface water sample (collected on 23 August 2016) at Analysesenteret, Trondheim, Norway

Parameter	**Value**
Surface area (km^2)	47
Mean depth (m)	138
Maximum depth (m)	309
Altitude (m a.s.l.)	251
Maximum regulation amplitude (m)	3.6
pH*	7.27
Turbidity (NTU)*	0.27
Total nitrogen ($\mu g\ l^{-1}$)*	180
Total phosphorus ($\mu g\ l^{-1}$)*	4.1
Total organic carbon ($mg\ l^{-1}$)*	2.9
Colour*	20

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642 **Table 2** Summary of the mean ± SD values, ranges (min–max) and between-year statistical comparisons (*t*-tests) of standard length, condition,
643 $\delta^{13}C$ and trophic position (TP) of brown trout, whitefish and grayling caught with survey gillnets before (2007) and after (2016) the smelt
644 introduction to Storsjøen. Statistically significant differences ($P < 0.05$) for *t*- and Mann-Whitney-Wilcoxon-tests (marked with *) are
645 highlighted in bold

Species	**Parameter**	**2007**			**2016**			**Statistics**	
		n	**Mean ± SD**	**Range**	**n**	**Mean ± SD**	**Range**	***t* / *W****	***P***
Brown trout	Length (mm)	72	258 ± 85	135 – 560	54	243 ± 79	140 – 518	2146*	0.322
	Condition	12	0.92 ± 0.08	0.79 – 1.19	15	0.92 ± 0.10	0.71 – 1.13	0.14	0.888
	$\delta^{13}C$ (‰)	12	-24.3 ± 2.2	-27.6 – -19.7	15	-26.9 ± 2.2	-30.1 – 22.5	3.01	**0.006**
	TP	12	2.36 ± 0.70	1.39 – 3.51	15	2.17 ± 0.43	1.15 – 2.97	0.84	0.412
Whitefish	Length (mm)	364	284 ± 101	100 – 414	100	315 ± 70	115 – 438	16162*	0.086
	Condition	364	0.82 ± 0.10	0.60 – 1.14	100	0.81 ± 0.11	0.45 – 1.06	18346*	0.547
	$\delta^{13}C$ (‰)	15	-28.5 ± 1.1	-30.1 – 26.5	40	-28.2 ± 2.1	-30.4 – -22.6	322*	0.685
	TP	15	2.46 ± 0.14	2.22 – 2.82	40	2.34 ± 0.32	0.98 – 2.87	369*	0.199
Grayling	Length (mm)	47	270 ± 88	112 – 440	21	318 ± 67	178 – 457	-2.81	**0.006**
	Condition	9	0.81 ± 0.11	0.60 – 0.99	21	0.80 ± 0.10	0.59 – 1.17	1028*	0.236
	$\delta^{13}C$ (‰)	9	-20.5 ± 2.5	-25.6 – -18.7	21	-22.1 ± 1.6	-27.7 – 20.1	1.81	0.098
	TP	9	2.02 ± 0.09	1.93 – 2.22	21	1.94 ± 0.29	1.58 – 2.42	107*	0.602

646

647 **Table 3** Model selection table based on AICc values for three candidate linear
648 regression models exploring trophic position (TP) and littoral reliance (LR) of brown
649 trout in Storsjøen. The most supported models (i.e. the most parsimonious models with
650 ΔAIC <2) are highlighted in bold. See Table 4 for summaries of the most supported
651 models and Fig. 5 for graphical visualization of the model outputs, illustrating brown
652 trout ontogenetic niche shifts before (2007) and after (2016) the smelt introduction

Model	**df**	**AICc**	**ΔAIC**
TP ~ log (Length) + Year + log (Length) x Year	**5**	**37.2**	**0**
TP ~ log (Length) + Year	4	41.6	4.4
TP ~ log (Length)	3	54	16.8
LR ~ log (Length) + Year	**4**	**-39.5**	**0**
LR ~ log (Length) + Year + log (Length) x Year	5	-37.7	1.8
LR ~ log (Length)	3	3.1	42.6

653

Table 4 Summary of the most supported models (see Table 3) predicting brown trout trophic position ($F_{3,51}$ = 84.2, R^2_{adj} = 0.82, P < 0.001) and littoral reliance ($F_{2,54}$ = 61.4, R^2_{adj} = 0.68, P <0.001) as a function of year (included as a factor) and log-transformed length (mm). Statistically significant parameters (P <0.05) are highlighted in bold. See Fig. 5a,b for graphical visualization of the model results, demonstrating ontogenetic dietary shifts of brown trout before (2007) and after (2016) the smelt introduction

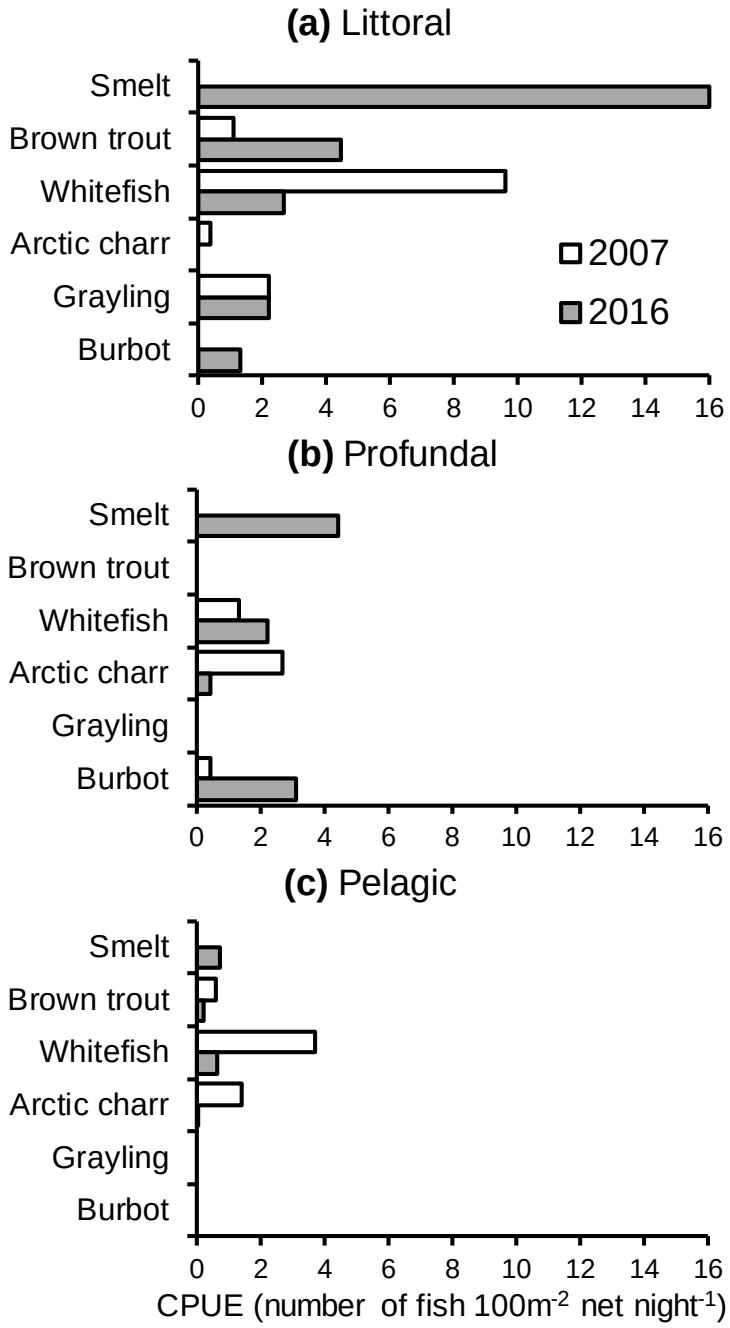
Response	**Parameter**	**Estimate**	**SE**	***t***	***P***
Trophic position	Intercept	–6.58	1.20	–5.47	**<0.001**
	Year	–3.68	1.57	–2.34	**0.020**
	(log) Length	1.55	0.20	7.67	**<0.001**
	(log) Length x Year	0.68	0.26	2.60	**0.010**
Littoral reliance	Intercept	3.56	0.35	10.10	**<0.001**
	Year	–0.39	0.05	–8.04	**<0.001**
	(log) Length	–0.46	0.06	–7.89	**<0.001**

661 **Table 5** Summary of the linear model ($F_{4,172}$ = 368.3, R^2_{adj} = 0.89, P <0.001), predicting
662 brown trout length in the year of capture (y) as a function of year (a factor with two
663 levels, 2007 and 2016), back-calculated length (Length $_{y-1}$) and age (Age $_{y-1}$) in the
664 previous year (y–1), and the interaction between the two latter explanatory variables
665 (Length $_{y-1}$ x Age $_{y-1}$). Statistically significant parameters (P <0.05) are highlighted in
666 bold. See Fig. 6 for graphical visualization of brown trout growth patterns before (2007)
667 and after (2016) the smelt introduction

Parameter	**Estimate**	**SE**	***t***	***P***
Intercept	29.02	16.87	1.72	0.087
Year	37.87	6.02	6.29	**<0.001**
Length $_{y-1}$	1.17	0.09	12.72	**<0.001**
Age $_{y-1}$	4.60	4.27	1.08	0.280
Length $_{y-1}$ x Age $_{y-1}$	–0.03	0.01	–2.13	**0.034**

668

669 **Figures**



670

671 **Fig. 1** Abundance of dominant fish species in Storsjøen before (2007) and after (2016)

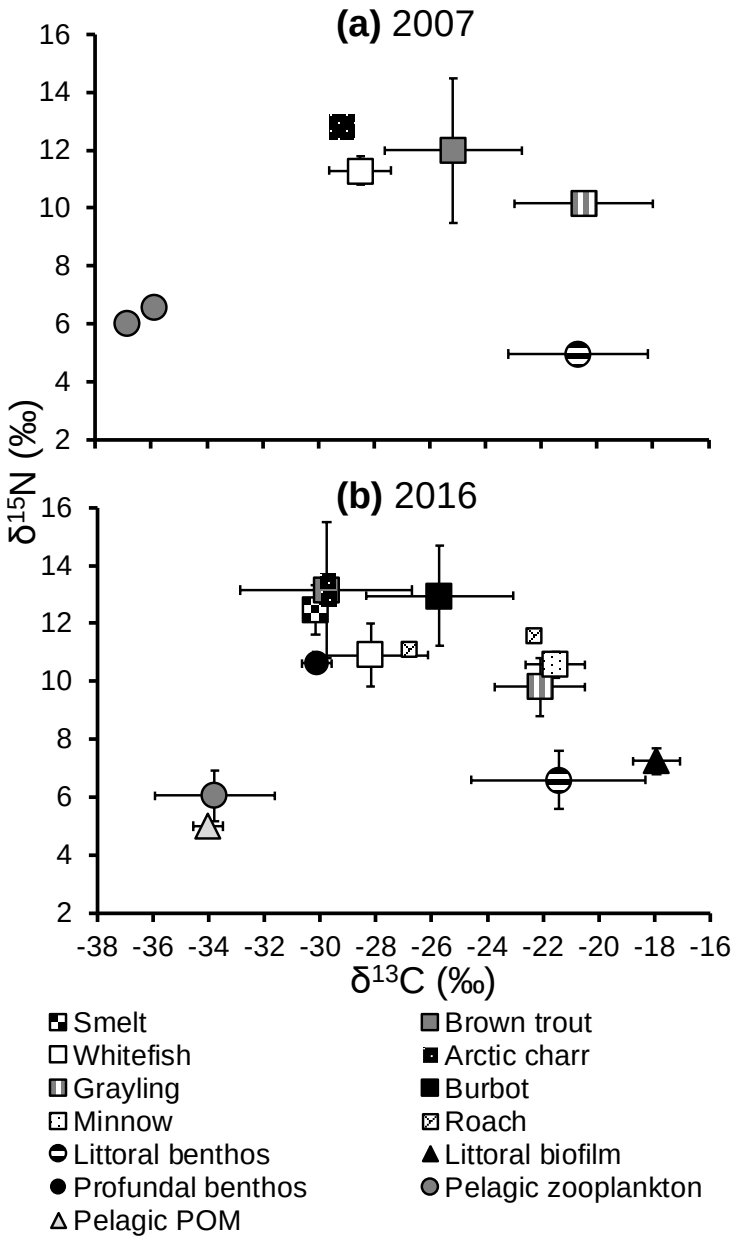
672 smelt introduction, based on catch per unit of effort (CPUE; number of fish $100m^{-2}$ net

673 $night^{-1}$) estimates from survey fishing in (A) littoral, (B) profundal and (C) pelagic

674 habitats. The CPUE estimates in (A) and (B) are based on benthic Nordic gillnet catches

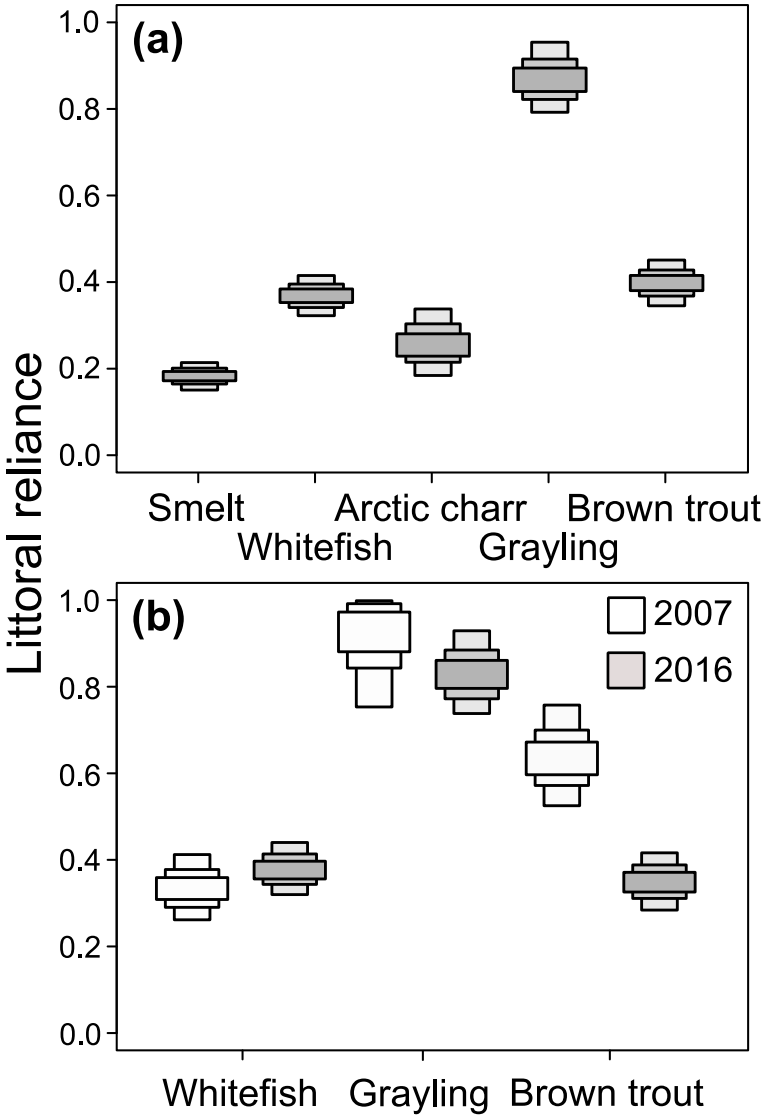
675 in June, whereas CPUE in (C) are based on catches in pelagic standard gillnets with

676 12–55 mm mesh set in June and August/September 2007 and 2016.



677

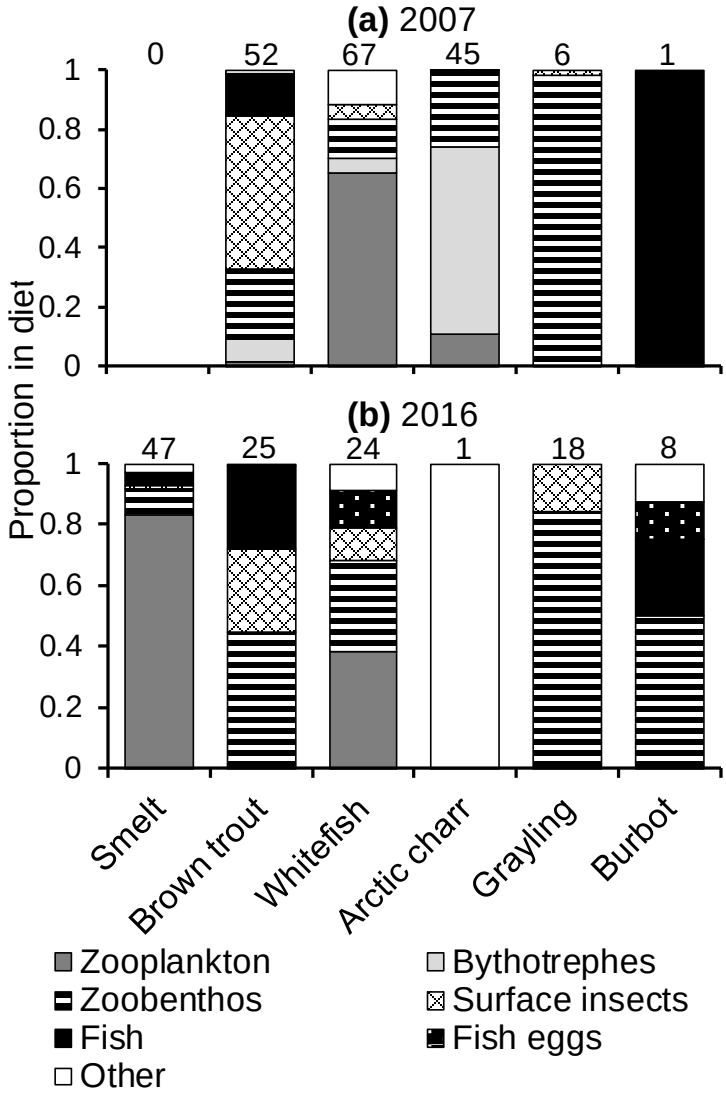
678 **Fig. 2** Stable isotope biplot showing the mean ± SD $\delta^{13}C$ and $\delta^{15}N$ values of littoral and
679 pelagic basal resources, invertebrates and different fish species collected from Storsjøen
680 (A) before and (B) after smelt introduction. Individual values are shown for the two
681 zooplankton samples analysed in 2007 and for the two Arctic charr and roach analysed
682 in 2016.



683

684 **Fig. 3** (a) Between-species and (b) between-year comparisons of littoral reliance of
685 different fish species in Storsjøen, based on results from SIAR two-source isotopic
686 mixing model. The boxes indicate the 95, 75 and 50% Bayesian credibility intervals for
687 the source proportion estimates

688

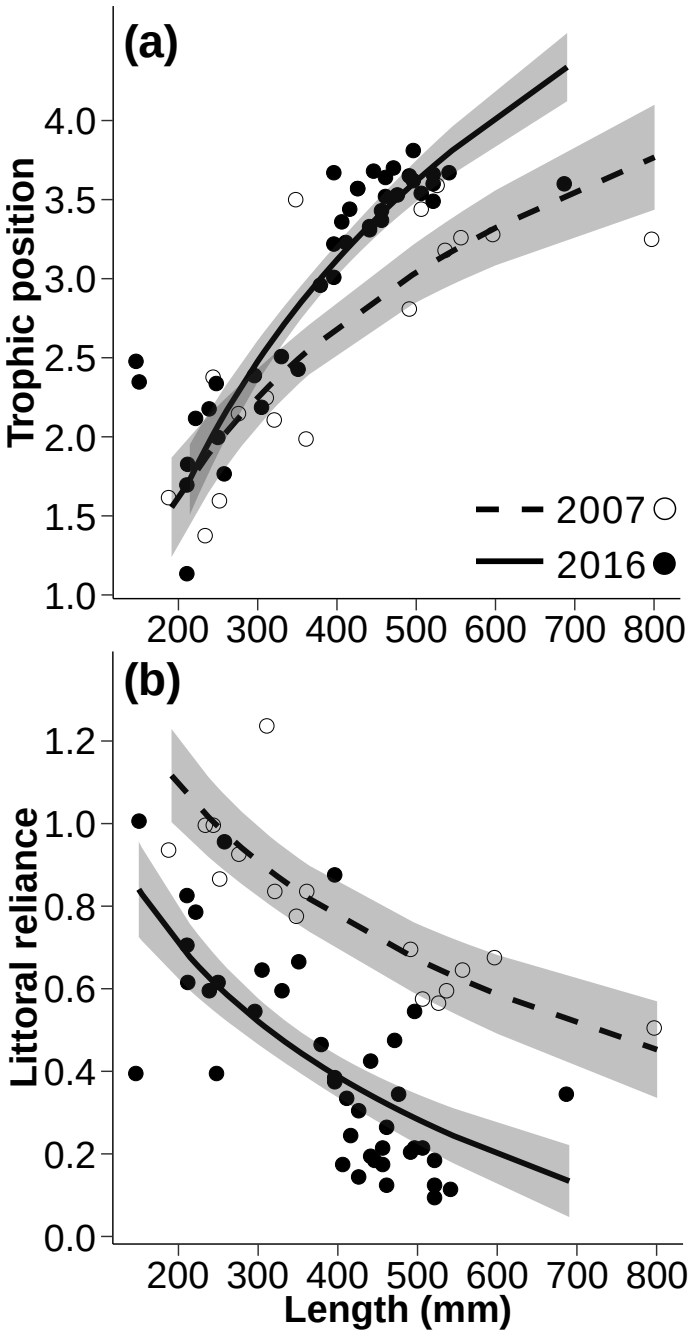


689

690 **Fig. 4** Proportion of different prey taxa in the stomach contents of dominant fish species

691 collected (a) before and (b) after the smelt introduction in Storsjøen. The numbers of

692 analysed fish are shown above the bars



693

694 **Fig. 5** Ontogenetic shifts in (A) trophic position and (B) littoral reliance of brown trout
695 caught from Storsjøen before (2007) and after (2016) smelt introduction. The lines
696 present predicted values from the most supported models for the 2007 (dashed line,
697 open circles) and 2016 (solid line, closed circles) data, based on linear models with year
698 (included as a factor) and log-transformed length (mm) as explanatory variables (see

699 Tables 3 and 4). The grey shadings depict the 95% confidence intervals for the predicted

700 TP and LR estimates

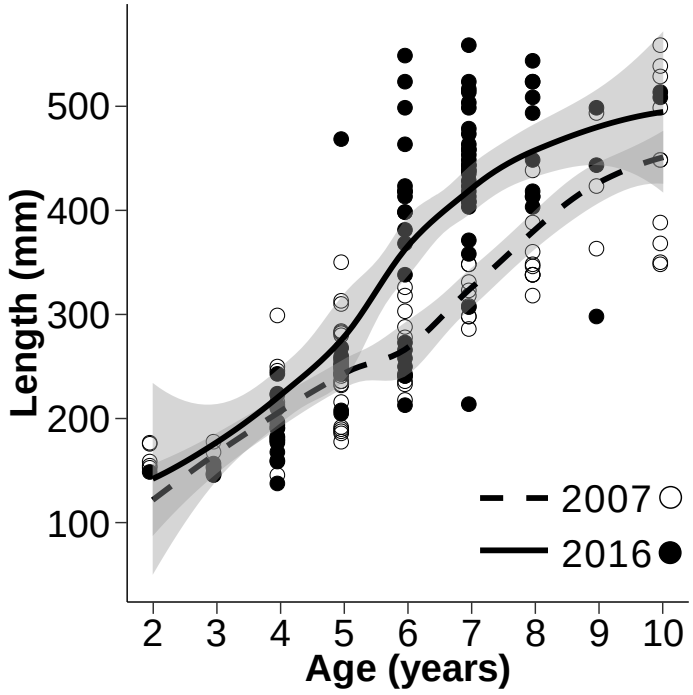


Fig. 6 Growth patterns of brown trout before (2007) and after (2016) the smelt introduction to Storsjøen. The lines show predicted lengths for the 2007 (dashed line, open circles) and 2016 (solid line, closed circles) data, based on a linear model with year as well as back-calculated length and age in the previous year and their interaction as explanatory variables (see Table 5). The grey shadings depict the 95% confidence intervals for the predicted lengths